

AN EMENDATION OF THE GENUS *SATHODRILUS* HOLT 1968  
(ANNELIDA: BRANCHIOBDELLIDA), WITH THE DESCRIPTION  
OF FOUR NEW SPECIES FROM THE PACIFIC DRAINAGE  
OF NORTH AMERICA

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As new species of a taxon are discovered and described, it is inevitable that generic concepts must be refined and extensions of range revealed. The genus *Sathodrilus* Holt, 1968, is emended, its relationships and distribution briefly discussed, a key to known species presented and four new species of the genus from the Pacific drainage of the northwestern region of the United States are described in this report.

The methods I use have been explained before (Holt, 1960; Hoffman, 1963, *inter alia*) and need not be repeated. The anatomical terminology used in the taxonomic treatment of the branchiobdellids has been defined (Holt, 1960; 1968b) and the usage thus established is followed herein. All illustrations are arranged with the anterior portion of any part to the reader's right and were done with the aid of a camera lucida. All measurements are approximations and the minimal and maximal measurements of specimens are given in parentheses after the average. The principal features of the reproductive systems are identified in Fig. 4.

Holotypes are deposited in the collections of the National Museum of Natural History (identified with the initials "USNM"); all other materials are in the collections of the Center for Systematics Collections, Virginia Polytechnic Institute and State University (identified with the initials "PCH"). Unless otherwise indicated, all collections used were taken by Virgie F. Holt and me.

To my knowledge there are only five references in the literature of science to the genus *Sathodrilus* (Holt, 1968b; 1969; 1973a; 1973b; 1975), and the last (1975) is in error in stating that members of *Oedipodrilus* Holt, 1967, occur in the northwestern United States.

The collecting of material upon which this paper is based was supported by the National Science Foundation (G9828). I am deeply indebted to my wife, Virgie F. Holt, for her untiring assistance during a laborious tent-camping expedition, to George C. Miller and to Horton H. Hobbs, Jr., for the identifications of the host crayfishes and to Dr. Hobbs for a careful reading of the manuscript.

*Sathodrilus* Holt, 1968b

*Type-species*.—*Sathodrilus carolinensis*, by original designation.

*Diagnosis*.—Small to medium-sized worms with 2 pairs of testes; unpaired

nephridiopore on dorsum of segment III; spermiducal gland with vasa deferentia entering entally; prostate absent, or prostatic protuberance or prostate, if present, incompletely divided from spermiducal gland; ejaculatory duct present; penis eversible, attached by cytoplasmic strands to inner wall of penial sheath; bursal atrium eversible; spermatheca with or without ental process (emended from Holt, 1968b).

*Remarks.*—The original diagnosis is emended primarily by deletions: three new species below have lobed peristomia (though not tentacles, of the upper lip); a prostate, though “incompletely divided” from the spermiducal gland, is present in all the species described below and one other (Holt, 1973:33).

The distinguishing feature of the genus is the structure of the eversible penis and bursal atrium. My earlier discussions (Holt, 1968b:294–295; 1969:196, 204–2–5) of the affinities of the genus stand as of now, though further studies of the branchiobdellids of the southeastern uplands of the United States, including the Ozark Plateau, may possibly modify these conclusions. But the nature of the penial complex may confuse the unwary: in members of such genera as *Cambarincola* the bursal atrium everts and the penis is protruded as a densely muscular cone (Fig. 1A); in species of *Sathodrilus*, not only does the bursal atrium evert, but so does the penis as a variably shaped double-walled cuticular tube that extends somewhat beyond the rim of the everted bursal atrium (Fig. 1B); in members of *Oedipodrilus*, the bursal atrium does not evert and the penis is an exceedingly long, thin cuticular tube, with or without “hooks,” that is free of the inner wall of the penial sheath of the bursa (Fig. 1C).

Many immediately obvious characters of the branchiobdellids are apparently the product of parallelism. Dorsal ridges of some body segments, dorsal projections of various forms, lobes and tentacles of the upper lip (the peristomium is usually, but not invariably divided into lower and upper lips), among other features, are found in many otherwise unrelated genera. The species of *Sathodrilus* reinforce the conviction that the structure of the male reproductive system is the most reliable basis for generic distinctions within the order.

My speculations as to the phylogenetic relationships of the branchiobdellids (Holt, 1968a; 1969), and my concepts of what constitutes a genus of the branchiobdellids, may or may not stand. In any case, with the four new species presented in this study, bringing the total number of species assigned to the genus to 11, we have before us a coherent group of forms and some speculation about their relationships and geographical history is now possible. Quite tentatively, I propose what follows.

The branchiobdellid evolutionary line which I have dubbed the “*Sathodrilus*-lineage” (Holt, 1969:197) is characterized by a single anterior nephridiopore and the ental junction of the vasa deferentia into the spermi-

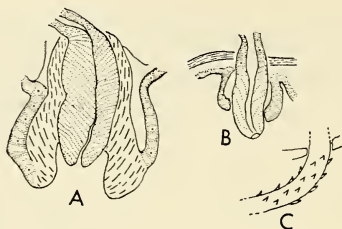


Fig. 1. Penial types. A, Cambarincoloid; B, Sathodriloid; C, Oedipodriloid (See text).

ducal gland. Despite the doubts I now entertain about the placement of genera within the *Sathodrilus* lineage, the latter character and the absence of a prostate or the presence of a rudiment of one (the "prostatic protuberance") are primitive features. Thus *Sathodrilus* remains as the most primitive member of its lineage and, further, it is possible, on the basis of the presence of prostatic protuberances and prostates, to place the species of *Sathodrilus* into three informal "sections." Three species, *Sathodrilus veracruzicus*, Holt, 1968b, *S. hortonii*, Holt, 1973b, and *S. okaloosae*, Holt, 1973a, lack even the rudiment of a prostate. Three other species, *S. carolinensis*, Holt, 1968b, *S. megadenus*, Holt, 1968b, and *S. villalobosi*, Holt, 1968b, have prostatic protuberances. Five species, *S. prostates*, Holt, 1973b, *S. dorfus*, new species, *S. lobatus*, new species, *S. norbyi*, new species, and *S. virgiliae*, new species, have prostate glands. The three species without a prostate are known from Florida and Mexico; those with prostatic protuberances from South Carolina, Georgia and Mexico; the third group with prostates are from Mexico and the Pacific drainage. These facts are consonant with the previously expressed speculations (Holt, 1968a; 1969; 1973b) that place the origin of branchiobdellid genera in late Cretaceous-early Cenozoic times in an area near or within the southern Appalachians.

And, though the hosts (all astacids) of the worms described herein are primitive, the Pacific Coast members of *Sathodrilus* are the more "advanced" of their congeners (except for the Mexican *S. prostates*). The paucity of locality records and the distinct possibility of the occurrence of other species of *Sathodrilus* in the Pacific drainage of the United States precludes any discussion of geographic relationships among those described below or any worthwhile attempt to devise a phylogenetic scheme for them beyond the informal one outlined above.

#### Key to Species of the Genus *Sathodrilus*

1	Prostate or prostatic protuberance absent	9
1'	Prostate or prostatic protuberance present	2

- 2(1') Prostate present 3
- 2' Prostate represented by rudimentary prostatic protuberance borne on spermiducal gland 7
- 3(2) Peristomium expanded, campanulate, upper lip distinctly lobed, Oregon and Washington *Sathodrilus lobatus*, new species
- 3' Peristomium subequal to head in diameter, upper lip with indistinct lobes or none 4
- 4(3') Spermatheca with prominent ental process and spermathecal bulb, dorsal ridge on segment VIII, Mexico *Sathodrilus prostates*
- 4' Spermatheca variable, dorsal ridge present or absent from segment VIII 5
- 5(4') With dorsal ridge on segment VIII, wall of spermathecal bulb very thick, no ental process of spermatheca, Idaho and Washington *Sathodrilus norbyi*, new species
- 5' Without dorsal ridges 6
- 6(5') Spermiducal gland and prostate combined subequal to bursa in length and diameter, ental process of spermatheca present, Oregon *Sathodrilus dorfus*, new species
- 6' Prostate subequal to spermiducal gland in diameter and greater than  $\frac{1}{2}$  length of latter, both combined exceeding length and diameter of bursa, spermatheca without ental process, Oregon and Washington *Sathodrilus virgiliae*, new species
- 7(2') Spermiducal gland exceeding body diameter in length, Georgia *Sathodrilus megadenus*
- 7' Spermiducal gland much shorter than body diameter 8
- 8(7') Bursa less than body diameter in length, spermatheca with short ectal duct and long clavate bulb, South Carolina *Sathodrilus carolinensis*
- 8' Bursa exceeding body diameter in length, spermatheca with long, narrow ectal duct and globose bulb, Mexico *Sathodrilus villalobosi*
- 9(1) Bursa exceeding body diameter in length, spermatheca without ental process, Mexico *Sathodrilus veraacruzicus*
- 9' Bursa less than body diameter in length 10
- 10(9') Bursa very short, about  $\frac{1}{4}$  body diameter, spermatheca with prominent spermathecal bursa, spermathecal bulb slender, cylindrical, Florida *Sathodrilus hortonii*
- 10' Bursa about  $\frac{2}{3}$  body diameter in length, spermatheca with long ectal duct, short bulb, long ental process, Florida *Sathodrilus okaloosae*

*Sathodrilus dorfus*, new species

Fig. 2

*Type-specimens*.—Holotype, USNM 53643, and 3 paratypes, PCH 1120, taken on *Pacifastacus leniusculus klamathensis* (Stimpson, 1857) from a small tributary to the Yaquina River, 13.4 km NE of Toledo, Lincoln Co., Oregon, 12 July 1960.

*Diagnosis*.—Small, slender worms (holotype, 2.0 mm); body outline smooth; upper lip with 4 blunt lobes, lower with 2; no oral papillae; jaws small, lightly colored, dental formula  $5/4$ ; bursa pyriform, about  $\frac{2}{3}$  body diameter in length, penial sheath about  $\frac{1}{3}$  total bursal length; spermiducal gland about  $\frac{2}{3}$  body diameter in length, its diameter  $\frac{2}{3}$  its length, without deferent lobes; prostate present about  $\frac{1}{2}$  spermiducal gland in length; spermatheca long, exceeding body diameter in length, ectal duct long, ental process present.

*Etymology*.—The name of this species is best regarded as an arbitrary combination of letters.

*Description*.—Only 4 specimens of *Sathodrilus dorfus* are known and they vary little in size, from approximately 1.9 to 2.3 mm in length. The holotype, the second smallest of the specimens has the following dimensions in mm: total length, 2.0; greatest diameter, 0.3; head length, 0.3; head diameter, 0.2; diameter, segment I, 0.2; diameter, sucker, 0.1.

The body outline is smooth. The clitellum is not prominent, but detectable. The nephridiopore is clearly located on the dorsum of segment III. The upper lip bears 4 short, blunt and indistinct lobes; the lower 2. Oral papillae are absent. The jaws are small, but rather darker than usual for their size. The dental formula is  $5/4$  but the lateralmost teeth are essentially impossible to detect in lateral view.

The spermiducal gland is short and thick, though the ectal portion narrows at its junction with the ejaculatory duct. The prostate is about  $\frac{1}{3}$  the length of the spermiducal gland and is subequal to the latter in diameter throughout its length. A prostatic bulb cannot be detected.

The ejaculatory duct is perhaps somewhat shorter than in its congeners, but along its midlength is thick-walled.

The penial sheath region of the bursa appears proportionately shorter than is usual in the genus. The penis is difficult to see in the specimens studied, but there is little doubt of its similarity in general conformation to that of other members of the genus. The bursal atrium is unremarkable.

The spermatheca is provided with an ental process in the holotype that is thick-walled and less in diameter than the median bulbar portion of the organ. Since the ental process bends dorsally over the gut, it is impossible in whole mounts to determine its relative length and it is not illustrated (Fig. 2). The spermathecal bulb is slightly greater in diameter than the

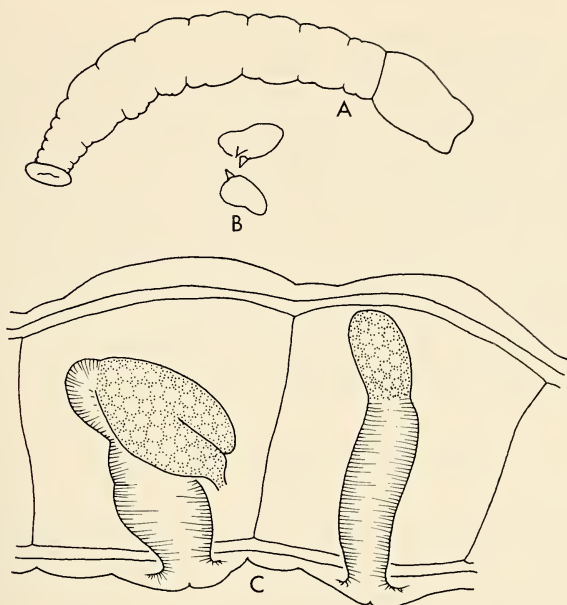


Fig. 2. *Sathodrilus dorfus*, new species; holotype. A, Outline of entire animal; B, Lateral view of jaws; C, Lateral view of reproductive systems.

ectal duct. The length of the latter is over half the diameter of segment V and lacks an ectal bulb.

*Variations.*—The only detectable variations among the four available specimens concern the spermatheca. In one paratype, the spermathecal bulb is expanded and broadly clavate and apparently without an ental process. The reality of ental processes of the spermathecae of some branchiobdellids is called into question by such observations, but the universal absence of ental processes in some species and the consistent occurrence of them in others confers some degree of reality to the structure other than a mere stage in development or the reproductive condition of the animal. Yet the latter probably does account for the differences in shape of the spermathecae of *S. dorfus*. The subject calls for further study.

*Affinities.*—All members of the genus *Sathodrilus* from the Pacific drainage of the United States and *S. prostates* from Puebla and Veracruz, Mexico, possess a prostate. But, as noted, the interspecies variations among these forms are of such a nature that it is not possible to propose any convincing phylogenetic theory for them. The "affinities" of *S. dorfus* and its congeners described in this paper are simply summary statements of the most striking ways in which each is distinct from the other members of the genus with prostates, though all differ to some degree in most of the taxonomically important features of the reproductive systems.

*Sathodrilus prostates* differs from all of the species treated herein in the presence of an obscure prostatic bulb and the elaborate differentiation of its spermatheca into four or more distinct "regions" (Holt, 1973b:33-34).

*Sathodrilus dorfus* lacks the prominent raised dorsal ridge of segment VIII of *S. norbyi*. The lobes of its upper lip are only four and its peristomium is not expanded in contrast to the six prominent lobes (plus others medially and ventrally) of the upper lip and the expanded peristomium of *S. lobatus*. The modest proportions of its spermiducal gland, prostate and spermatheca, among other features, distinguishes it from *S. virgiliae*.

*Hosts*.—*Pacifastacus leniusculus klamathensis*.

*Distribution*.—Known only from the type-locality.

*Material examined*.—The type-series.

*Sathodrilus lobatus*, new species

Fig. 3

*Type-specimens*.—Holotype and 3 paratypes, USNM 53644, and 5 paratypes, PCH 1117, taken on *Pacifastacus leniusculus klamathensis* from Mary's River, 7.7 km E of Blodgett, Benton Co., Oregon, 12 July 1960.

*Diagnosis*.—Small, slender worms (holotype, 2.0 mm); body outline smooth, slightly raised dorsal ridge on segment VIII; peristomium expanded, campanulate; upper lip with 6 lobes, lower with 2, 3 lateral lobes on each side, total peristomium with 14 lobes; no oral papillae; jaws small, brown, dental formula 5/4, median teeth of lower jaw widely separated; bursa subcylindrical, large, exceeding  $\frac{2}{3}$  diameter of segment VI in length, penial sheath composing about  $\frac{1}{2}$  total bursal length; ejaculatory duct with thick, muscular midportion; total length of spermiducal gland greater than body diameter, prostate about  $\frac{1}{3}$  to  $\frac{1}{2}$  spermiducal gland in length; spermatheca long, exceeding twice body diameter, ectal duct muscular, spermathecal bulb expanded, ental process long, latter 2 subequal in length.

*Etymology*.—Latin, *lobatus*, furnished with lobes, for the large number of lobes on the expanded peristomium.

*Description*.—*Sathodrilus lobatus* is composed of relatively small worms. Five specimens have the following dimension in mm: total length, 2.3 (2.2-2.7); greatest diameter, 0.3 (0.3-0.4); head length, 0.4 (0.4-0.5); head diameter, 0.2 (0.2-0.2); diameter, segment I, 0.2 (0.2-0.2); diameter, sucker, 0.2 (0.2-0.2). The holotype has the following dimensions: total length, 2.6; greatest diameter, 0.4; head length, 0.5; head diameter, 0.2; diameter, segment I, 0.3; diameter, sucker, 0.3.

The body outline is smooth, but careful examination reveals a weakly raised dorsal ridge on segment VIII. As usual in small worms, the anterior nephridiopore is obscure, but can be detected on the dorsum of segment III. The expanded peristomium is distinctive and immediately identifies the

species. Greatly expanded and bell-shaped, it is only weakly divided into upper and lower lips and is furnished with more lobes than any other American branchiobdellid. The lobes are difficult to count in the holotype, but a paratype, mounted with the ventral side uppermost, has 6 dorsal lobes, 3 lateral ones on each side and 2 prominent ventral ones: 14 in all. Oral papillae are absent. The jaws are not unusually prominent, but distinctly brown. The dental formula of  $5/4$  is also difficult to determine in lateral aspect. The median teeth of the lower jaw are widely, for the size of the jaw, separated; the lateral teeth of both jaws are small and obscure.

The spermiducal gland is long, extending from the ventral border of the coelom dorsad and then bending sharply to extend the length of segment VI to its junction with the ejaculatory duct, decreasing noticeably in diameter as it does so. Its length is such that it is impossible to adequately represent its character in two dimensions (Fig. 3). The prostate, subequal to the ental third of the spermiducal gland in diameter is subequal in length to this ental portion of the latter. The histology of neither shows any peculiarities, but the prostate is separated from the spermiducal gland beyond its origin.

The ejaculatory duct is long, narrowed at each end, and expanded into a striking muscular bulb along its midlength. This midportion of the duct is composed of 2 distinct layers: an outer thick one of radial muscles; an inner one of what appear to be a continuation of the longitudinal (in reference to the organ) muscles. The illustration (Fig. 3) departs from the semi-diagrammatic nature of most of my drawings in attempting to represent the arrangement of these 2 layers of muscles.

The penial sheath comprises slightly more than half the total length of the bursa and is not noticeably lesser in diameter than the bursal atrium. The entire bursa is slightly more than  $\frac{2}{3}$  the diameter of the segment and otherwise conforms to the structure of the bursae of most members of the genus (cf. *S. villalobosi*, Holt, 1968b). The penis is prominent and its ectal part normally extends into the bursal atrium, filling the lumen of the latter.

The spermatheca is distinctive. The ectal muscular duct is, as usual for members of the genus, long, extending dorsad to the dorsal border of the gut. There it expands into a thin-walled spermathecal bulb which appears to be a fluid-filled space with a hardly detectable quantity of spermatozoa present. Entally, the organ continues as a long ental process running cephalad along the dorsal border of the segment and often bending to extend ventrad along septum  $\frac{1}{2}$ . The ental process possesses a lumen that in some cases, at least, contains spermatozoa, unusual, if true, but it is composed principally of a lining of tall glandular cells with their inner (lumen-facing) ends directed towards the spermathecal bulb.

*Variations.*—No variations of significance have been detected. There is the expected degree of differences in the degree of expansion of the peristo-



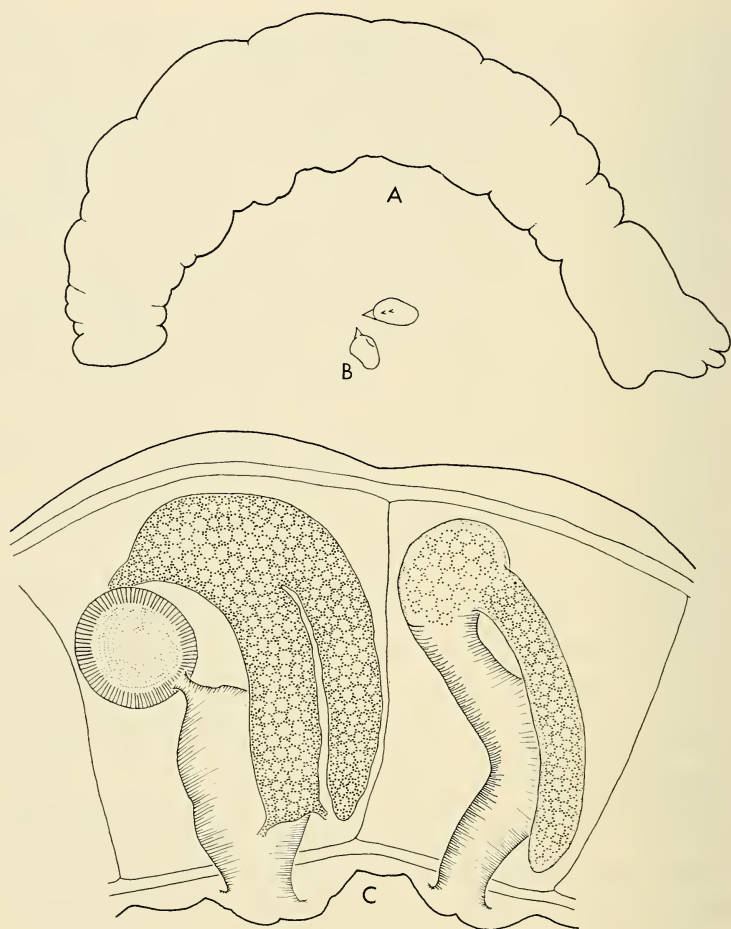


Fig. 3. *Sathodrilus lobatus*, new species, holotype. A, Outline of entire animal; B, Lateral view of jaws; C, Lateral view of reproductive systems.

mium, the exact position and angle at which components of the reproductive system lie, uncertainty as to whether the ental process of the spermatheca always contains spermatozoa, and often the difficulty of determining the presence of a dorsal ridge on segment VIII. The latter, however, is certain; dorsally, there are supernumerary muscles present on the dorsum of VIII that are absent on the dorsa of other segments.

*Affinities.*—*Sathodrilus lobatus* is readily distinguished from all other members of the genus by the campanulate peristomium which bears numerous distinct lobes. Its spermiducal gland and prostate are proportionately larger than those of *S. norbyi* and *S. dorfus* and distinctly smaller than those

of *S. virgiliae*. The spermatheca of *S. lobatus* has a distinctive median thin-walled bulb and a long, prominent, thick-walled ental process (cf. Figs. 2, 4, 6).

*Hosts*.—*Pacifastacus leniusculus klamathensis*.

*Distribution*.—Streams of the Costal Range in Oregon and Washington and of the Willamette Valley in Oregon.

*Material examined*.—The type-series; OREGON: 10 specimens, PCH 1129, taken on *P. l. klamathensis* from trib. Yaquina River, 25 km E Toledo, Lincoln Co., 12 July 1960; 9 specimens, PCH 1120, taken on *P. l. klamathensis* from Siletz River, 9.7 km E Toledo, Lincoln Co., 12 July 1960; 6 specimens, PCH 1121, taken on *P. l. klamathensis* from Siletz River, 39 km S Kernville, Lincoln Co., 12 July 1960; 1 specimen, PCH 1123, taken on *P. l. klamathensis* from Widow Creek near Rose Lodge, Lincoln Co., 13 July 1960; 8 specimens, PCH 1124, taken on *P. l. klamathensis* from South Yamhill River, 2.6 km W Valley Junction, Polk Co., 13 July 1960; 5 specimens, PCH 1125, taken on *P. l. klamathensis* from Salt Creek, 5.6 km NW Dallas, Polk Co., 13 July 1960; 4 specimens, PCH 1126, taken on *P. l. klamathensis* from Little Pudding Creek, 13.9 km SW Silverton, Polk Co., 13 July 1960; 10 specimens, PCH 1128, taken on *P. l. klamathensis* from Salmon River at Brightwood, Clackamas Co., 13 July 1960. WASHINGTON: 9 specimens, PCH 1129, taken on *P. l. klamathensis*, 7.7 km SE Skamokawa, Wahkiakum Co., 14 July 1960; 5 specimens, PCH 1131, taken on *P. l. klamathensis* from Middle Nemah River, 1.6 S Nemah, Pacific Co., 14 July 1960; 4 specimens, PCH 1132, taken on *P. l. klamathensis*, from West Fork Hoquiam River, 23.3 km S Humptulips, Grays Harbor Co., 16 July 1960; 10 specimens, PCH 1133, taken on *P. l. klamathensis* from Humptulips River at Humptulips, Grays Harbor Co., 16 July 1960; 5 specimens, PCH 1134, taken on *P. l. klamathensis*, 4.9 km S Amanda Park, Grays Harbor Co., 16 July 1960; 6 specimens, PCH 1136, taken on *P. l. trowbridgii* from Nolan Creek, 34.6 km S Forks, Jefferson Co., 16 July 1960; 4 specimens, PCH 1137, taken on *P. l. trowbridgii* from Mill Creek at Forks, Clallam Co., 16 July 1960; 3 specimens, PCH 1139, taken on *P. l. trowbridgii* from Minter Creek, 6.3 km W Wauna, Pierce Co., 17 July 1960.

*Sathodrilus norbyi*, new species

Fig. 4

*Type-specimens*.—Holotype and 3 paratypes, USNM 53642, and 15 paratypes, PCH 920, taken on *Pacifastacus leniusculus klamathensis* from Union Flat Creek, about 13 km W of Pullman, Whitman Co., Washington, 11 July 1958, by Darwin E. Norby.

*Diagnosis*.—Small, slender worms (holotype, 1.6 mm in length); segment VIII with prominent dorsal ridge; lips entire, no oral papillae; jaws

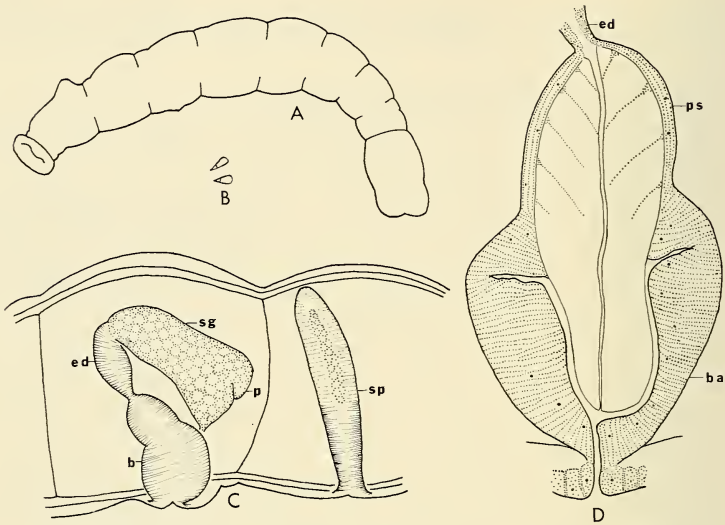


Fig. 4. *Sathodrilus norbyi*, new species, holotype. A, Outline of entire animal; B, Lateral view of jaws; C, Lateral view of reproductive systems; D, Optical longitudinal section of bursa and penis. Abbreviations: b, bursa; ba, bursal atrium; ed, ejaculatory duct; p, prostate; ps, penial sheath; sg, spermiducal gland; sp, spermatheca.

small, delicate, light brown, dental formula  $5/4$ ; bursa pyriform, approximately  $\frac{1}{2}$  body diameter in length, penial sheath about  $\frac{2}{3}$  total bursal length; length of spermiducal gland about  $\frac{3}{4}$  body diameter, its width  $\frac{3}{4}$  its length, without deferent lobes; prostate small lobe of ental end of spermiducal gland; spermatheca with long ectal duct, long cylindrical bulb, latter with thick wall, no ental process, length of total organ equal to or greater than body diameter.

*Etymology.*—It is a pleasure to dedicate this species to its discoverer and my friend, Dr. Darwin E. Norby.

*Description.*—Specimens of *Sathodrilus norbyi* are small worms. Five types, including the holotype, have the following dimensions in mm: total length, 1.6 (1.3–2.0); greatest diameter, 0.2 (0.2–0.2); head length, 0.3 (0.2–0.3); head diameter, 0.2 (0.2–0.2); diameter, segment I, 0.2 (0.2–0.2); diameter, sucker, 0.2 (0.2–0.2).

The body outline is smooth, except for a prominent dorsal ridge on segment VIII. The clitellum is quite clearly distinct on both segments VI and VII; somewhat better developed on segment VII. The single anterior nephridiopore is difficult to detect, but opens on the dorsum of segment III. The lips are undivided into lobes, there are no discernable oral papillae and no external sulci of the head. The jaws are small. The lateral teeth are difficult or impossible to see in lateral view, but there is no doubt that

the dental formula is 5/4. As usual for such small jaws, they are also light in color, a yellow-brown.

The spermiducal gland is relatively large and thick, but presents no peculiarities other than the very obscure prostate which is separated from the spermiducal gland by a slight cleft at the dorso-ental border of the latter and often, apparently, encloses a minute clear space.

The ejaculatory duct is proportionately large, though short, with a thick muscular wall.

The penial sheath portion of the bursal complex is cylindrical with a relatively thin muscular wall which encloses a penis that is composed of a thin membrane (Fig. 4D). The ectal portion of the penis is usually partly everted, and when so, fills the large bursal atrium. The ental part of the penis is connected to the inner wall of the penial sheath by a few thin strands that can only be seen with certainty in sections. The atrial portion of the bursa, with heavy muscular walls, composes over half of the entire organ.

The spermatheca lacks an ental process. The spermathecal bulb is usually cylindrical and its wall is thick, its inner lining composed of glandular cells of greater than usual height (projecting further into the lumen of the bulb). The ectal duct is long and muscular with very large muscle cells composing an ectal bulb or sphincter.

*Variations.*—Other than the usual differences in the positions in which portions of the male organs may lie in the coelom and the possible absence of lateral teeth in some specimens (a doubtful point), the only significant variation concerns the spermathecal bulb. In some specimens it is expanded and markedly greater in diameter than the inner part of the ectal duct. Yet spermathecae with unexpanded bulbs contain spermatozoa and those that are expanded seem to be filled with a clear fluid.

*Affinities.*—*Sathodrilus norbyi* is readily recognized by the dorsal ridge on segment III. This character and an apparent prostatic bulb relates it to *S. prostates*, though the prostate of the latter is much more prominent. Among its neighbors in the Pacific drainage, it and *S. virgiliae* lack an ental process of the spermatheca, but the prostate of *virgiliae* is large and does not adhere throughout its length to the spermiducal gland. *S. dorfus* and *S. lobatus* both have an ental process of the spermatheca and more distinctly developed prostates, though the latter are not as large as that of *S. virgiliae*.

*Hosts.*—*Pacifastacus leniusculus klamathensis*.

*Distribution.*—Snake River drainage in Idaho and eastern Washington; Yakima River drainage in Washington.

*Material examined.*—The type-series, 5 sectioned animals from the type-locality; IDAHO: 5 specimens, PCH 924, taken from St. Maries River, about 3 km NW Clarkia, Shoshone Co., on *Pacifastacus leniusculus klamathensis* by D. E. Norby, 21 June 1959. WASHINGTON: 7 specimens (PCH 1142) taken in a warm pool, 7.6 km E Ellensburg, Kittitas Co., 18 July 1960.

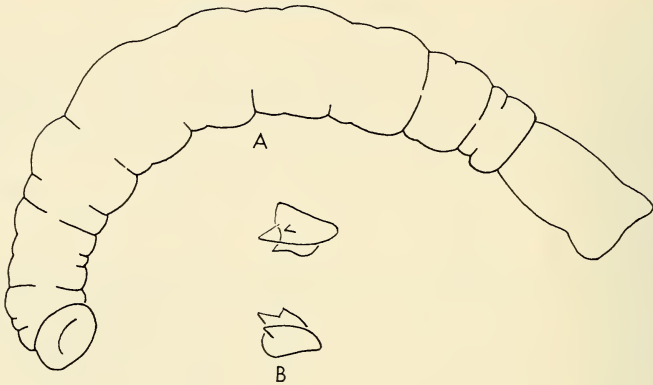


Fig. 5. *Sathodrilus virgiliae*, new species, holotype. A, Outline of entire animal; B, Latero-oblique view of jaws.

*Remarks.*—I have one specimen (PCH 1142) from the Kittitas County, Washington, collection, in which the spermiducal gland is reduced to a few glandular cells with no sign of a prostatic protuberance. This may simply represent an aberrant variant of *S. norbyi*, but it is probably a representative of a different species and students should be aware of this.

*Sathodrilus virgiliae* new species

Figs. 5-7

*Type-specimens.*—Holotype, USNM 53645, and 6 paratypes, PCH 1116, taken on *Pacifastacus leniusculus klamathensis* from Marys River at Philomath, Benton Co., OREGON, 12 July, 1960.

*Diagnosis.*—Small, slender worms (holotype 2.5 mm); body outline smooth, segment VIII with obscure dorsal ridge with minute supernumerary muscles; upper lip with 4 short lobes, lower lip entire; no oral papillae; jaws small, light brown, dental formula 5/4; bursa long, cylindrical, slightly greater than  $\frac{2}{3}$  body diameter in length, penial sheath about  $\frac{1}{2}$  total bursal length; spermiducal gland large, approximately twice the body diameter in length; prostate about  $\frac{1}{2}$  spermiducal gland in length, usually not adherent to latter; spermatheca with long ectal duct; long spermathecal bulb, no ental process.

*Etymology.*—It is with dutiful gratitude that I dedicate this species to my wife who has assisted me in so many ways in my study of the branchiobdellids. Her given name is the anglicized feminine diminutive of the Latin *Virgil*.

*Description.*—The average dimensions of the holotype and 4 paratypes of *S. virgiliae* in mm are as follows: total length, 2.2 (2.1-2.5); greatest

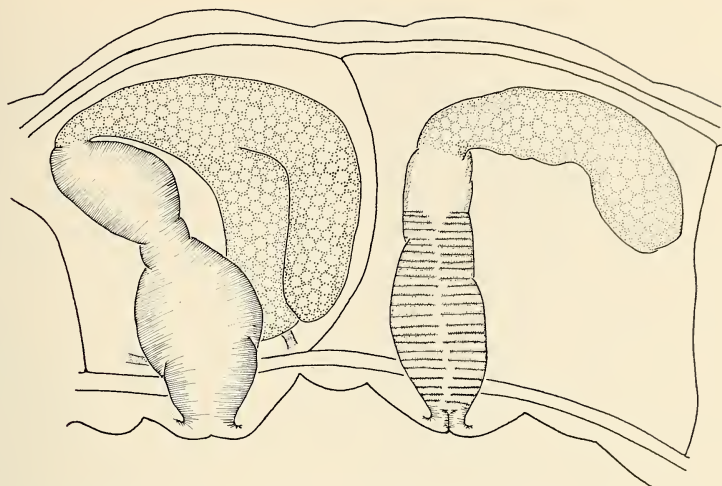


Fig. 6. *Sathodrilus virgiliae*, new species, holotype. Lateral view of reproductive systems.

diameter, 0.3 (0.3–0.3); head length, 0.3 (0.3–0.4); head diameter, 0.2 (0.2–0.2); diameter, segment I, 0.2 (0.2–0.2); diameter, sucker, 0.2 (0.2–0.2).

The body outline is smooth, with segment VIII bearing a very slightly raised dorsal ridge. The clitellum and anterior nephridiopore are not unusually prominent. The upper lip bears 4 blunt, short lobes; the lower is entire. There are no oral papillae. In some specimens there is a shallow sulcus encircling the head. The jaws are relatively small, light brown, with a dental formula of  $5/4$ , though the lateral teeth are small and difficult to detect.

The spermiducal gland is remarkable for its length and size. It has no obvious deferent lobes and slightly narrows ectally. It extends from the ventral to the dorsal border of its segment, bends sharply to run posteriorad along the dorsal border of segment VI and then ventrad to its junction with the ejaculatory duct, decreasing in diameter along its ectal portion.

The prostate arises from the spermiducal gland about one-third the length of the latter from its ental end and is unique in that it rarely lies against the spermiducal gland beyond its junction with the latter, but rather in various positions within the coelom (Fig. 7). Its apparent normal position in the illustration of the holotype is an artifact of perspective: the prostate diverges from, but lies laterad to the spermiducal gland (Fig. 6).

The ejaculatory duct, narrow at each end, is expanded into a heavily muscular "bulb" along its midlength.

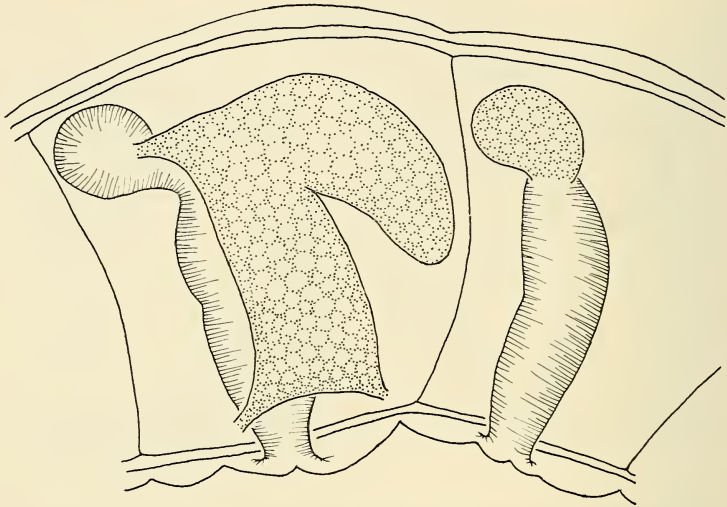


Fig. 7. *Sathodrilus virgiliae*, new species. Lateral view of reproductive systems of a paratype.

The penial sheath region of the bursa is prominent and its inner wall is lined with a layer of cells of indeterminate character. The penis is distinctly membranous, arises at the ental end of the penial sheath and continues as a clearly distinct cuticular tube into the bursal atrium. No strands connecting the penis to the wall of the penial sheath are detectable, but the penis is not the thin, coiled (within the penial sheath) one of species of *Oedipodrilus*.

The spermatheca consists of a long ectal duct, a thin-walled median part and a bulb approximately equal to the ectal duct in length which in fully mature specimens gradually increases in diameter toward its ental end. Spermatozoa are not obvious within the median part; it appears to be filled with a clear fluid.

*Variations.*—The dorsal ridge of segment VIII is often obscured and is easily overlooked, but a very thin supernumerary muscle layer is present. The spermathecal bulb is not expanded in some specimens. The positions assumed by the spermatheca, the prostate, the spermiducal gland and the ejaculatory duct (all of which are proportionately very large) vary (? because of their size) and present, initially, confusing patterns.

*Affinities.*—*Sathodrilus virgiliae* is readily separated from *S. prostates*, *S. dorfus*, *S. lobatus*, and *S. norbyi* by its large prostate, which diverges from its place of origin on the spermiducal gland. The latter is also remarkably long, exceeding in length that of the bursa and the diameter of the body. Only *S. megadenus*, among the species of *Sathodrilus*, has a spermiducal

gland of such prominence, but *megadenus* has no prostate, only a small and obscure prostatic protuberance (Holt, 1968b).

*Hosts.*—*Pacifastacus leniusculus klamathensis*.

*Material examined.*—OREGON: the type-series; one specimen, PCH 1114, taken on *P. l. klamathensis* from Row River, 3.2 km E Cottage Grove, Lane Co., 11 July 1960; 31 specimens, PCH 1115, taken on *P. l. klamathensis* from Coast Fork of Willamette River, 24.3 km S Eugene, Lane Co., 11 July 1960; 14 specimens, PCH 1118, taken on *P. l. klamathensis* at Burnt Woods, Lincoln Co., 12 July 1960; 7 specimens, PCH 1121, taken on *P. l. klamathensis* from Siletz River, 38.9 km SE Kernville, Lincoln Co., 12 July 1960; 5 specimens, PCH 1125, taken on *P. l. leniusculus* from Salt Creek, 5.6 km NW Dallas, Polk Co., 13 July 1960; 18 specimens, PCH 1127, taken on *P. l. leniusculus* from Butte Creek, 9.6 km NW Silverton, Marion-Clackamas Co. line, 13 July 1960; 5 specimens, PCH 1128, taken on *P. l. klamathensis* from Salmon River at Brightwood, Clackamas Co., 13 July 1960. WASHINGTON: 16 specimens, PCH 1140, taken on *P. l. klamathensis* from Kachess Lake, 22.4 km NW Cle Elum, Kittitas Co., 18 July 1960; 11 specimens, PCH 1141, taken on *P. l. klamathensis* from Teenaway River, 30.5 km NW Ellensburg, Kittitas Co., 18 July 1960.

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